Predictions of Taylor's power law, density dependence and pink noise from a neutrally modeled time series

Petr Keil [a,*], Tomáš Herben [b,c], James Rosindell [d], David Storch [a,e]

[a] *Department of Ecology, Faculty of Science, Charles University, Vinicna 7, 12844 Praha 2, Czech Republic*
[b] *Institute of Botany, Academy of Sciences of the Czech Republic, Průhonice, 252 43, Czech Republic*
[c] *Department of Botany, Faculty of Science, Charles University, Benátská 2, Praha 2, 128 01, Czech Republic*
[d] *Institute of Integrative and Comparative Biology, Faculty of Biological Sciences, University of Leeds, Leeds LS2 9JT, United Kingdom*
[e] *Center for Theoretical Study, Charles University in Prague and the Academy of Sciences of the Czech Republic, Jilská 1, 110 00 Praha 1, Czech Republic*

ARTICLE INFO

ABSTRACT

There has recently been increasing interest in neutral models of biodiversity and their ability to reproduce the patterns observed in nature, such as species abundance distributions. Here we investigate the ability of a neutral model to predict phenomena observed in single-population time series, a study complementary to most existing work that concentrates on snapshots in time of the whole community. We consider tests for density dependence, the dominant frequencies of population fluctuation (spectral density) and a relationship between the mean and variance of a fluctuating population (Taylor's power law). We simulated an archipelago model of a set of interconnected local communities with variable mortality rate, migration rate, speciation rate, size of local community and number of local communities. Our spectral analysis showed 'pink noise': a departure from a standard random walk dynamics in favor of the higher frequency fluctuations which is partly consistent with empirical data. We detected density dependence in local community time series but not in metacommunity time series. The slope of the Taylor's power law in the model was similar to the slopes observed in natural populations, but the fit to the power law was worse. Our observations of pink noise and density dependence can be attributed to the presence of an upper limit to community sizes and to the effect of migration which distorts temporal autocorrelation in local time series. We conclude that some of the phenomena observed in natural time series can emerge from neutral processes, as a result of random zero-sum birth, death and migration. This suggests the neutral model would be a parsimonious null model for future studies of time series data.

© 2010 Elsevier Ltd. All rights reserved.

1. Introduction

The neutral theory of biodiversity (NTB; Hubbell, 2001; Chave, 2004; Alonso et al., 2006; Leigh, 2007; Rosindell et al., 2010) has revolutionized the way we think about species coexistence over the last decade. The assumptions of the theory are controversial (Tilman, 2004; Leibold and McPeek, 2006) and some argue that there is limited empirical support (McGill et al., 2006), but the theory still has huge potential as a null model (Gotelli and McGill, 2006), serving as an essential first approximation to reality and a base for more complex theories. Even with its apparently over-simplified set of assumptions, the NTB is capable of predicting realistic species-abundance distributions (Hubbell, 2001; Etienne, 2005) and species-area curves (Rosindell and Cornell, 2007, 2009),

as well as many other ecological patterns (Herben et al., 2004; Herben, 2009). Most of the current research is focused on the community-level predictions of a single snapshot in time at equilibrium (McGill, 2003; Turnbull et al., 2005; Volkov et al., 2005; Dornelas, et al., 2006). Dynamical behaviour of populations in NTB has rarely been studied. Azaele et al. (2006) used ratios of population sizes between two snapshots of time to estimate species turnover rates and extinction times of trees in Barro Colorado Island, Panama. Mutshinda et al. (2008) produced the only study (as far as we are aware) that examines sufficiently long real-world time series from the perspective of NTB. They used the Bayesian statistical framework and a neutral model of community dynamics (zero-sum assumption relaxed) to show that sizes of natural communities fluctuate more than expected under neutrality. However, Mutshinda et al. (2008) focused only on the dynamics of local community size and they did not examine time series of individual species.

There are some characteristics of natural time-series that are often used as summary statistics and can be employed here in

* Corresponding author.
E-mail addresses: pkeil@seznam.cz (P. Keil), herben@site.cas.cz (T. Herben), j.l.rosindell@leeds.ac.uk (J. Rosindell), storch@cts.cuni.cz (D. Storch).

making comparisons with the time series produced by a neutral model. For example, natural time series have been shown to obey some degree of stabilizing density dependence (Woiwod and Hanski, 1992; Brook and Bradshaw, 2006; Sibly et al., 2007). Natural populations also follow a specific relationship between mean population size (m) and variance of population size (s^2) called Taylor's Power Law (TPL) (Taylor et al., 1983; Tokeshi, 1995; Ballantyne and Kerkhoff, 2007) which has the form $s^2 \propto m^b$. In natural populations, the exponent b of TPL is usually observed to satisfy $1 < b < 2$ (Kendal, 2004). Natural time series can be considered as being the net result of a number of independent fluctuations each with a distinct frequency and amplitude. The amplitude (or 'spectral density') $S(f)$ is a function of the frequency f and often satisfies $S(f) \propto 1/f^{\gamma}$ (Halley, 1996). The exponent γ usually falls between 0 and 2 for natural time series (Arino and Pimm, 1995; Halley, 1996; Inchausti and Halley, 2001, 2002), a property known as 'pink noise'.

The null model for discrete population dynamics is an unbounded *random walk* of population size (N) and is described as

$$\ln N_{t+1} = \ln N_t + e_t \qquad (1)$$

where e_t varies at random according to a given distribution with zero mean and is independent of population size (Murdoch, 1994; Hanski et al., 1996). The model is a discrete first-order Markov chain in which all the information that can influence the future state ($t+1$) is fully captured in the present state (t). Random walk time series are often termed 'brownian' or autocorrelated noise. Random walk is synonymous for a completely density-independent process in ecology, it produces a slope of $b \approx 2$ in Taylor's power law and spectral scaling exponent of $\gamma \approx 2$.

Although the term random walk is sometimes used to describe the population time series in neutral models (Hubbell, 2001; Alonso et al., 2006), there are reasons why neutral models can behave differently from the random walk as defined above. Firstly, there is usually a constraint on the total number of individuals (the 'zero-sum' rule) which imposes a clear upper limit to any population fluctuations (Hubbell, 2001; Hubbell and Lake, 2003). Secondly, immigration of individuals into the local community can cause a locally extinct species to reappear (zero is not necessarily absorbing; Hubbell, 2001), and finally immigration can distort the temporal autocorrelation of N (the number of individuals belonging to the species of interest in a local community). In the presence of immigration, N_{t+1} for a given local community does not depend solely on N_t for that community (as in the autocorrelated random walk), it also depends on the N_t for all the other local communities (the metacommunity).

In this paper we ask if a simple neutral model can produce time series that are similar to natural time series. In particular, we show that populations in the neutral model can produce realistic slopes of the Taylor's power law, have spectral properties similar to natural populations and seem to reveal density-dependency more frequently than expected in a random walk. Additionally, we explore the influence of the NTB parameters (size of local communities, number of local communities, mortality rate, migration and mutation rate) on these properties of population time series.

2. Methods

2.1. The simulation model

Instead of the classic neutral model used by Hubbell (2001) and Volkov et al. (2003), we simulate a *metacommunity* consisting of an archipelago of L isolated *local communities* interconnected by migration at rate m (see Fig. 1 and Volkov et al., 2007). Each local
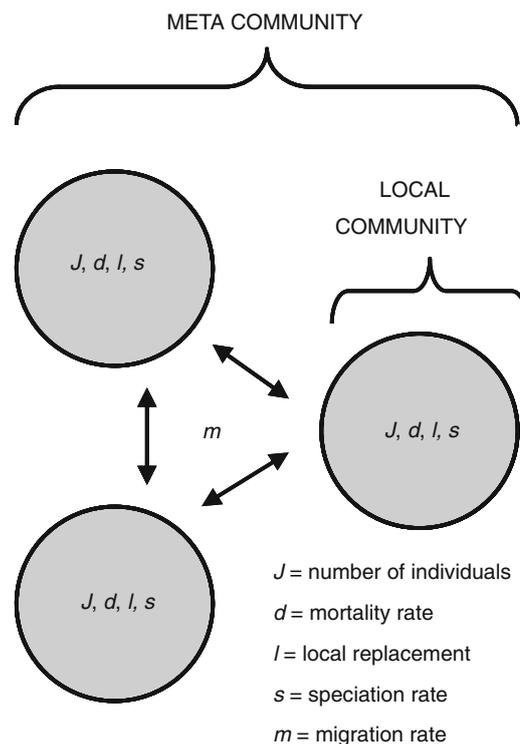

Fig. 1. Schematic illustration of the 'archipelago' model. Note that we performed our simulations using much larger numbers of local communities than illustrated here. See the Methods section for detailed description of the model.

community contains J individuals all of which behave in an identical manner irrespective of the species to which they belong. The archipelago model enabled us to obtain data on abundances and their variances for one species at multiple local communities, which is necessary for the analysis of Taylor's power law. We used the simulation approach because it enabled us to record the species identity of every individual at each time step and across all local communities. Furthermore, we wished to collect time series of limited lengths that are comparable to those of empirically collected time series in order to accurately mimic any sampling effects present in empirical data. This would be particularly difficult to approach analytically. Our simulations were conducted using a 'forwards in time' approach. A 'backwards in time' or coalescence approach can be much faster (Rosindell et al., 2008), but the main strengths of this approach are only present when collecting a snap shot in time of a sample from a very large or infinite metacommunity. We are instead collecting single species time series data and sampling all individuals from a relatively small metacommunity: a scenario where coalescence is far less beneficial.

Four processes operate in the local community at each step: mortality (d; $0 < d < 1$), local replacement (l; $0 < l < 1$), immigration from outside of the local community (m; $m = 1 - l$) and speciation (s; $0 < s < 1$) in that order (Fig. 1, Table 1). To model mortality, $J \times d$ individuals were randomly removed from each local community in every time step with all individuals having an equal probability of removal. These removed individuals were then replaced by offspring from others in the local community and other local communities (immigration). Local replacement was modeled by drawing individuals to reproduce at random from the $J(1-d)$ individuals that survived mortality until $J \times d \times l$ offspring have been created. The remaining $J \times d \times m$ dead individuals were replaced by immigration from all of the other local communities. The probability of immigration of a species is

Table 1
An overview of the parameters and their levels used in our neutral model simulations.

Parameter	Description	Levels used in simulations
Number of local communities (L)	Number of local communities that make up the metacommunity	100, 20
Size of each local community (J)	Number of individuals in each local community	2000, 500
Mortality rate (d)	Mortality rate of individuals per time step in the local community	0.6, 0.3
Migration rate (m)	Proportion of vacant positions in the community replaced by migration from other local communities	0.1, 0.3
Speciation rate (s)	Speciation rate per species per step	2×10^{-6}, 3×10^{-6}

See Material and methods section for detailed description of the exact function of each parameter.

given by its relative abundance in the whole metacommunity (excluding the local community in focus).

A local population can occasionally give rise to a new species (a speciation event), this happens with a fixed probability at each time step for each local population of a species. When speciation occurs, individuals of the given species in the local community were randomly split into two parts, one of which forms the initial abundance of a new species (a version of *random-fission* model; Hubbell, 2001; Etienne and Haegeman, in press; Haegeman and Etienne, 2010). Pilot testing of a *point mutation* model (Hubbell, 2001) showed that the choice of a speciation model does not affect the outcome of the simulations, this is not entirely surprising because for a single species population time series, speciation can be regarded as another form of mortality: individuals belonging to our focal species that switch to a new species reduce the population of our focal species in the same way as dead individuals. Each simulation was launched with only one species that occurred in all local communities and was left running for 5000 steps which we found was always sufficient for the system to reach a steady state. The last 100 steps of the simulation were then taken and used for analyses.

2.2. Spectral analysis

We performed 200 simulations for each combination of model parameters (Table 1). From each simulation we randomly selected one species and from this species we used two time series: (1) time series of population sizes within a randomly selected *local community* and (2) time series of population sizes within the whole *metacommunity*. In cases where the species went extinct in one or both time series we randomly selected another one thereby conditioning the time series as being drawn from a locally extant species. For these time series we conducted spectral analysis (Halley, 1996; Legendre and Legendre, 2003, pp. 680–681) and estimated the value of the exponent γ in $S(f) \propto 1/f^{\gamma}$ where $S(f)$ is spectral density at given frequency f ($0 \leq f \leq f_{n/2}$; n is length of the time series). Values of $S(f)$ were obtained through Fast Fourier Transform of the log-transformed time series data. The spectral exponent γ was estimated as minus the regression slope of the $\log(S(f))$ versus $\log(f)$. This procedure is exactly the same as used by Inchausti and Halley (2001) and hence our estimates of γ are directly comparable to theirs (Fig. 2). The value of γ can vary from $\gamma < 0$ ('blue noise') through $\gamma = 0$ ('white noise'), $\gamma \approx 1$ ('pink noise') and $\gamma = 2$ ('brown noise' or

random walk) to $\gamma > 2$ ('black noise'). We use the term 'whitening' of the spectra for a deviation of γ from 2 towards 0.

To assess the effects of the neutral model parameters on γ we fitted a multiple ANOVA model with γ as the response variable and five explanatory variables: mortality rate, migration rate, speciation rate, number of local communities and number of individuals. Since we were dealing with simulated data we only report R^2s and do not report any P-values because these could be modified arbitrarily by changing number of simulations. Comparisons were made with the values of γ measured in natural populations taken from the Global Population Dynamics Database (kindly provided by Pablo Inchausti; see also Inchausti and Halley, 2001, 2002).

2.3. Testing for density dependence

Using the same data, we conducted three distinct tests for density dependence in the time series: Pollard's randomization test (Pollard et al., 1987), Dennis and Taper's parametric bootstrap maximum likelihood test (PLBR; Dennis and Taper, 1994) and Bulmer's test (Bulmer, 1974). The Pollards's test is a distribution-free likelihood ratio randomization test in which a random walk (Eq. (1)) or a random walk with trend are density-independent hypotheses, whereas the density-dependent hypothesis is defined as a first-order *linear* autoregression model (stochastic Gompertz model):

$$\ln N_{t+1} = \ln N_t + r + \beta \ln N_t + e_t \quad (\beta \neq 1) \qquad (2)$$

where r and β are model parameters. The Bulmer's test is a parametric predecessor of the Pollard's test and has been criticized for weak performance in cases where there was a trend in the data ($r \neq 0$). The PLBR test is a likelihood ratio test which uses the first-order *non-linear* autoregression model (stochastic logistic model) as the density-dependent hypothesis:

$$\ln N_{t+1} = \ln N_t + r + \beta N_t + e_t \qquad (3)$$

All of these tests have been criticized for disputable performance when there is a census error affecting the estimation of population abundance in the field (Shenk et al., 1998; Freckleton et al., 2006), but this is not the case for our simulated data. All three tests gave nearly identical results and we therefore only present the output from Pollard's randomization test (Pollard et al., 1987) which is 'Pollard's P': the probability of observing the empirical data in the case of the density-independent hypothesis (Eq. (1)). Following the approach of Woiwod and Hanski (1992) we normalized the distribution of Pollard's P by logit transformation. To assess effects of the neutral model parameters on Pollard's P we again fitted a multiple ANOVA model in which we used the values of logit-transformed Pollard's P as the response variable.

2.4. Taylor's power law

To test if populations in our model obey the Taylor's Power Law (TPL) we performed 50 simulations for each combination of parameters (Table 1). For each species in the simulations we created a metapopulation matrix (MPM) of abundances in which rows represent the last 100 time steps of the simulation and columns represent the populations in different local communities. We excluded all MPMs in which the species had gone globally extinct. We studied the TPL in its temporal context (Taylor and Woiwod, 1982) which means that variances and means are calculated over each column (one column is one local population) in the MPM – when plotted, each point in the log-log plot therefore represents one local population. Using rows instead of columns in the MPM would yield the TPL in a spatial context, but
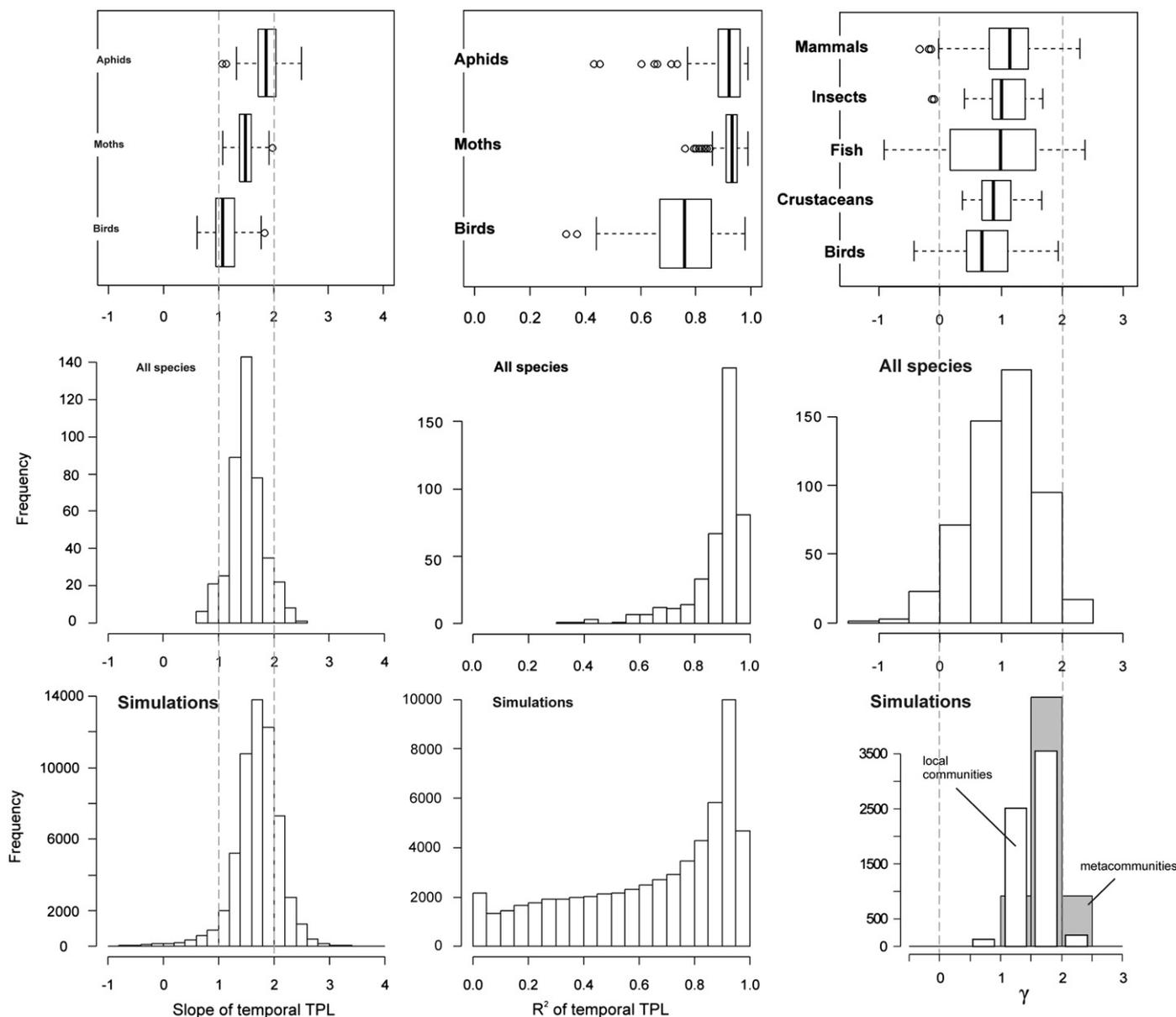
Fig. 2. Some aspects of real-world populations and those produced by our neutral model. Empirical slopes of Taylor's power law and coefficients of determination of TPL of 429 species of aphids, moths and birds were taken from Taylor and Woiwod (1980, 1982). Empirical values of scaling exponent γ of power spectra of 544 time series were taken from the Global Population Dynamics Database (GPDD, kindly provided by Pablo Inchausti; see also Inchausti and Halley, 2001, 2002). Box and whisker plots show medians, quartiles and outliers.

the temporal context is more germane to this time series study. A linear regression was fitted in each of the log-log plots and the TPL slope (parameter b; Taylor, 1961; Tokeshi, 1995) and the coefficients of determination (R^2) were calculated. As with our other results, the simulated values of TPL slopes and R^2s were compared with empirically observed values (taken from Taylor and Woiwod, 1980, 1982).

3. Results

3.1. Spectral analysis

Values of the scaling exponent γ estimated from our simulations are summarized in Fig. 2. For local communities, the median value of γ was 1.59 (2.5% and 97.5% quantiles were 1.26 and 2.19,

respectively). The value of γ was only influenced by mortality rate and migration rate (Table 2, Fig. 3) with higher mortality and higher migration, each producing time series that were closer to pink noise ($\gamma < 2$) (Fig. 2). On the metacommunity scale, the median of γ was 1.75 (2.5% and 97.5% quantiles were 1.05 and 2.07, respectively). We did not detect any influence of the model parameters on the value of γ at the metacommunity scale (Table 2, Fig. 3). Our simulations produced γ values falling within a narrower interval than is generally observed in nature (Fig. 2); however, they departed from 2 (the value for an unbounded random walk) in the same direction as for natural populations.

In general, the population time series emerging from our neutral model had lower γ than would be expected for an autocorrelated random walk ($\gamma = 2$). This could partly be an artifact caused by the insufficient length of time series. It was

Table 2
Strength of the effect of each parameter on the value of γ and the logit-transformed Pollard's P.

	Local communities		Metacommunities		
	R^2 (γ)	R^2 (logit of Pollard's P)	R^2 (γ)	R^2 (logit of Pollard's P)	R^2 (slope of TPL)
Mortality rate	**0.045**	**0.078**	< 0.001	< 0.001	**0.019**
Migration rate	**0.11**	**0.19**	< 0.001	< 0.001	**0.0014**
Speciation rate	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
# of local communities	< 0.001	**0.014**	< 0.001	< 0.001	**0.048**
Size of local community	< 0.001	< 0.001	< 0.001	< 0.001	**0.0015**

Parameter γ describes the 'color' of the spectra of a time series. Pollard's P is the probability of obtaining the data in case of density independence (random walk). The values of R^2 were estimated using a multiple ANOVA. Figures in bold show values higher than 0.001.
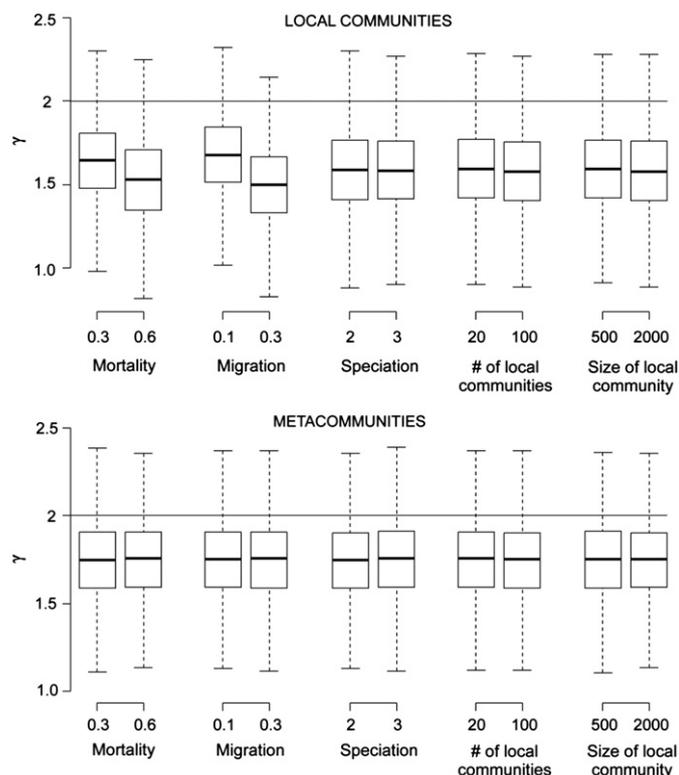
Fig. 3. Results of the spectral analysis of population time series produced by a neutral model. γ is the scaling exponent in $S(f) \propto 1/f^{\gamma}$ where $S(f)$ is spectral density and f is frequency. Displayed are the effects of the neutral model's parameters (Table 1) on γ as a box and whisker plot with median and quartiles. A random walk of sufficient length would have $\gamma = 2$.

recently shown that random walks of length ~100 actually give estimates of between 1.5 and 1.8 instead of 2 because of the missing low-frequency fluctuations (Miramontes and Rohani, 2002). Nevertheless, since empirically collected time series are rarely longer than 100 sequential observations, our simulations of time series of similar lengths are amply justified to purposefully include the effects of sampling over a limited time scale. Since we also showed that the vales of γ tended to be lower at local scales when comparing time series of equal lengths, we can still conclude that some whitening of spectra at local community sales is caused by more than just the length of the sampled time series.

3.2. Testing for density dependence

On the scale of local communities the median of Pollard's P was 0.14 (2.5% and 97.5% quantiles were 0 and 0.82, respectively)

indicating a distribution skewed towards the lower values of Pollard's P. We also found that the values of Pollard's P were dependent on mortality rate and migration rate (Table 2, Fig. 4). Similarly to spectral analysis, simulations with higher mortality rate and higher migration rate produced time series with lower values of Pollard's P (Fig. 4). On the metacommunity scale the median value of Pollard's P was 0.5 (2.5% and 97.5% quantiles being 0.01 and 0.97, respectively). This indicates no clear signal of density dependence on the metacommunity scale. We did not detect any influence of the other model parameters on the values of logit-transformed Pollard's P (Table 2, Fig. 4). Pollard's P varied with relative abundance of species in local communities but not in metacommunities (Fig. 6).

3.3. Taylor's power law (TPL)

The median slope of TPL was 1.73 (2.5% and 97.5% quantiles were 0.059 and 2.49, respectively). The coefficients of determination (R^2) of power law regressions varied, following skewed, non-normal distributions (Figs. 2 and 5), having generally lower values to what has been observed in nature (Fig. 2). The effects of model parameters on the slope of TPL was not as distinct as in spectral analysis and density dependence analysis; we detected a weak influence of number of local communities and mortality rate on the slopes of TPL (Table 2, Fig. 5). Both the slopes and R^2s showed negative dependence on the mean relative abundance of species (Fig. 7).

4. Discussion

4.1. Spectral analysis and density dependence

The observed whitening of spectra in our model is not what we would expect under random walk dynamics. One possible reason for this is the effect of *migration* which can cause the spectral whitening. A population in an isolated local community (low or no immigration from outside) follows dynamics similar to an autocorrelated random walk ($\gamma \approx 2$) in which there is little or no dependence on the abundances in other local communities. However, after introducing immigration from outside of the local community, the autocorrelative nature of the process is broken and the species abundance in the whole metacommunity becomes important. The influence of single local community dynamics on the metacommunity are likely to be small (inversely proportional to the number of local communities), but in contrast the influence of the metacommunity on local community dynamics can be substantial (proportional to the migration rate). Hence, the migration causes the local time series to be whitened (non-autocorrelated in time) while the metacommunity time series remains 'brownian' (autocorrelated in time). The *mortality* rate can also cause spectral whitening by adding random
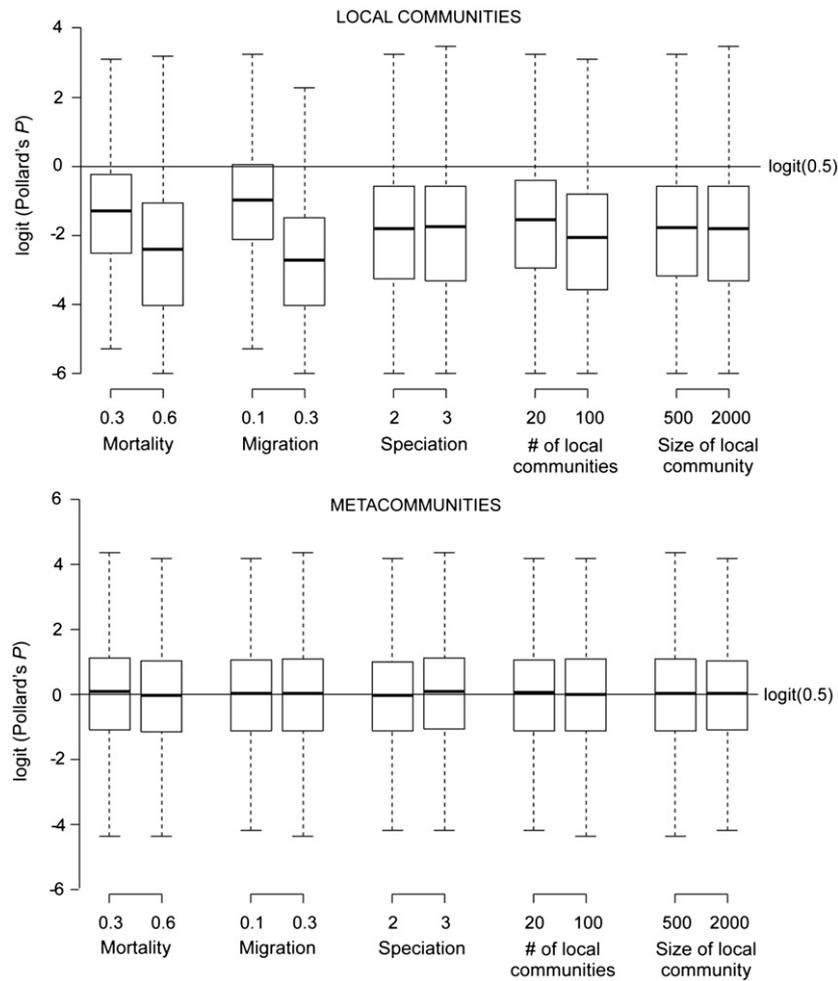
Fig. 4. Results of the testing for density dependence in population time series produced by neutral model as a box and whisker plot with median and quartiles. Pollard's P is the probability of obtaining the data in case of density independence (Eq. (1); Pollard et al., 1987).
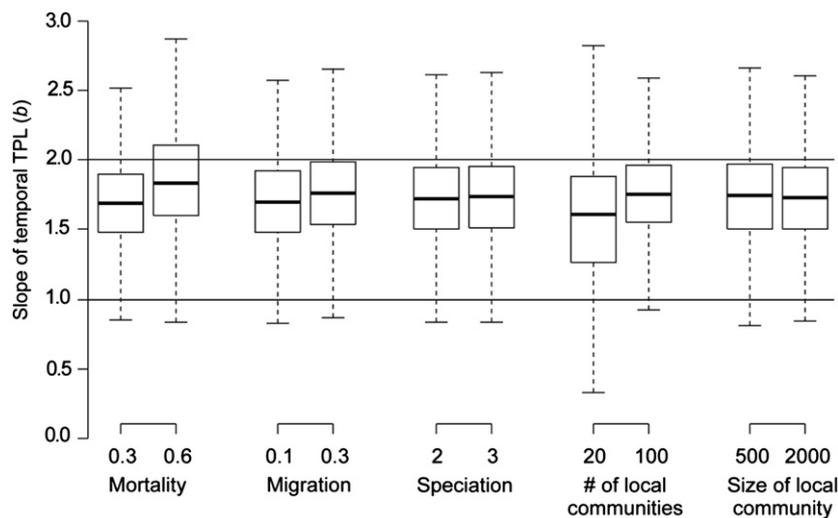
Fig. 5. The slopes of temporal Taylor's power law (TPL) as produced by neutral models with various levels of model parameters. Solid horizontal lines delimit the range observed in natural populations. Shown as a box and whisker plot with median and quartiles shown, outliers are not displayed.

population fluctuations at high frequencies, but not at low ones subsequently lowering γ. We expect that this effect of mortality rate would not be apparent in very long time series (> 400 time steps; Miramontes and Rohani, 2002). However, such long time

series are nearly never available in ecology and we wanted to keep our time series comparably long to the real-world ones.

The spectral analysis results are mirrored by the results of the tests for density dependence. Density dependence is modeled
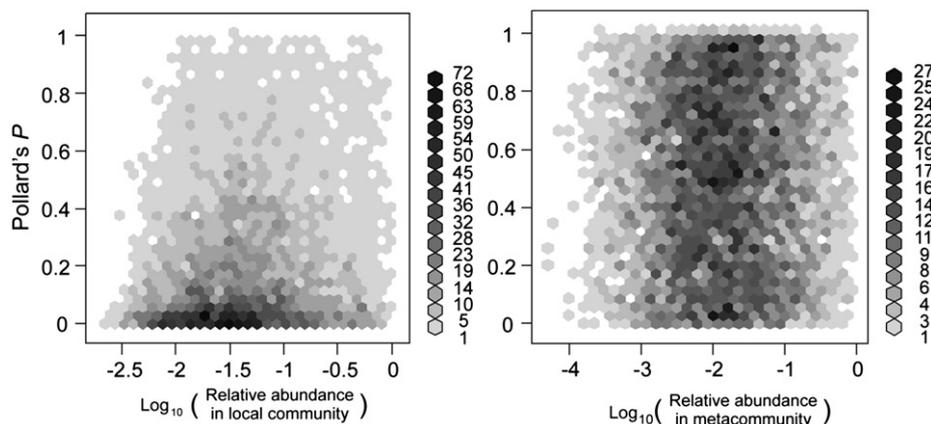
Fig. 6. Dependence of Pollard's P on relative abundance of species in local communities and in metacommunities. Shades of grey represent density of points in hexagonal bins.
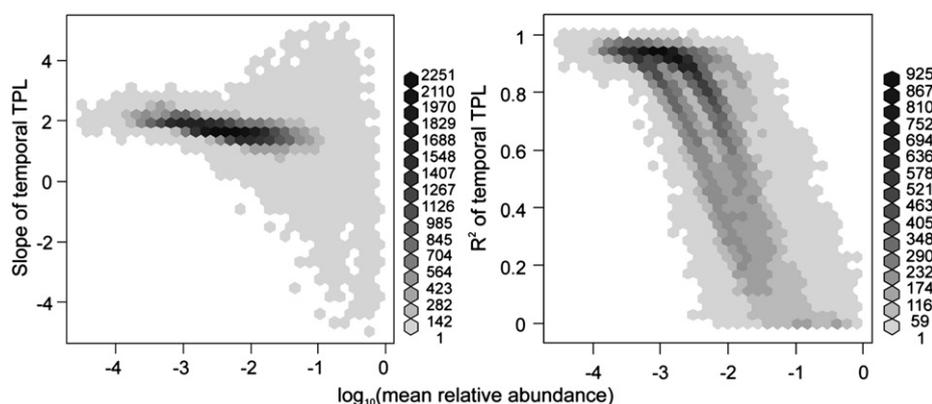

Fig. 7. Dependence of slope and coefficient of determination (R^2) of Taylor's power law on mean relative abundance of species in local communities. Shades of grey represent density of points in hexagonal bins.

either as stochastic Gompertz (Eq. (2)) or stochastic logistic (Eq. (3)) models in the tests we used (Shenk et al., 1998, see also Methods section).

It has been recognized for a long time (Eberhardt, 1970; Freckleton et al., 2006) that a sequence of uncorrelated random numbers ('white noise') tends to follow a pattern consistent with density dependence. If you take white noise time series and plot changes of ln population size ($\ln N_{t+1} - \ln N_t$) against $\ln N_t$ (where N_t is the number of individuals at time t) you will get a linear negative relationship, corresponding (spuriously) to the density-dependent Gompertz model (Eq. (2)) with $\beta \approx -1$. Moreover, white noise can be very similar to the output of the stochastic logistic model (Eq. (3)) with $\beta < 0$. We have learned that the whitening of a spectra means bringing it from $\gamma \approx 2$ down towards 0, which is white noise. We also know that migration (by breaking the autocorrelation structure) and mortality rate (by increasing spectral density at high frequencies in time series of limited length) cause spectral whitening. The detection of density dependence can also be attributed to the same mechanisms, although most ecologists would consider such density dependence to be spurious (Freckleton et al., 2006).

Uncorrelated noise in the form of census error also causes spurious detection of density dependence, which has long been known to population ecologists (Shenk et al., 1998; Freckleton et al., 2006). Moreover, Freckleton et al. (2006) showed an example of a population that follows a random walk but consists of two subpopulations each of which apparently shows density dependence because there is random migration between them.

That immigration can cause time series to resemble a sequence of uncorrelated random numbers was also noted by Anderson et al. (1982) and this is indeed the case for our neutral model.

There should also be real density dependence in our model. In an isolated community, the closer N_t gets to zero (extinction) or to J (monodominance) the lower the probability of N_{t+1} differing from N_t will be. When a species almost fills the local community, its probability of increasing its abundance in the next time step is small, because it is unlikely that one of the few individuals belonging to a different species will be selected for mortality. Similarly, when the abundance of a species is low, its probability of reproducing is low because after mortality it is not likely to be selected to reproduce. The highest rate of fluctuations and lowest incidence of density dependence is then expected when a population has a relative abundance of 0.5 (Hubbell, 2001). We detected this form of density dependence only in local communities at low relative abundances (Fig. 6). Species with high relative abundances were rare in our simulations and hence we were unable to clearly show the real density dependence for them (Fig. 6) even though in theory it must exist.

4.2. Taylor's power law (TPL)

The archipelago neutral model produced slopes of Taylor's power law with median close to the range observed in natural populations ($1 < b < 2$), but with higher incidence of low coefficients of determination. In order to explain this we need

to summarize the mean-variance scaling properties of simple stochastic models. If a species undergoes an unrestricted random walk (Eq. (1)), the TPL has a slope $b=1$ at very low population densities and gradually changes to $b=2$ at a certain density (Anderson et al., 1982; Tokeshi, 1995; Keeling, 2000). The population density at which b starts to change from 1 to 2 depends on the relative magnitude of stochastic changes because of the high incidence of extinctions at low population densities which lower the variance. This effect can explain $b<2$ at very low densities.

Hubbell (2001) shows what happens with the mean-variance scaling if the stochastic population fluctuations are restricted by an upper boundary (the zero-sum rule) and are fed by immigration, although Hubbell does not use the term Taylor's power law. Hubbell (2001) predicts hump-shaped parabolic relationship between abundance of species in a metacommunity and the variance of a local population size undergoing the zero-sum ecological drift. He also hypothesizes that most of the species in nature have low relative abundances and hence should occur in the left part (relative abundance <0.2) of the parabola which is nearly linear in the log-log space, resembling the power-law with slope of 2. Although Hubbell's (2001) reasoning focuses on the relationship between mean and variance in a set of species within one community (one point in the mean-variance plot represents one species) it can apply to the set of single-species local populations in our model: the mean relative abundances of species in local communities were rarely higher than 0.2 in our simulations and indeed, there is a much better fit of the TPL for species with low abundances (Fig. 7). The poor fit at higher relative abundances is then a result of fitting the linear TPL on the actually parabolic mean-variance relationship. Consequently, as the mean relative abundance of species increases, the slope of the TPL decreases (Fig. 7).

4.3. Comparison with empirical data and conclusions

Our model produces qualitatively similar patterns to those observed in nature. This is perhaps surprising given the assumptions made by the neutral model, but it does again highlight its use as a powerful null model.

There is a general agreement that natural time series are not 'brownian' (Fig. 1; Arino and Pimm, 1995; Inchausti and Halley, 2001, 2002) – they clearly fall into the whitened range of scaling exponents ($0<\gamma<2$; Fig. 2). Our simulations indicate that neutral models have the potential to explain part of this observed whitening, although this potential may be limited. Although higher migration rates can result in time series with more realistic values of γ, our migration rates are similar (10%) or much higher (30%) than what is usually observed in natural metacommunities (see Volkov et al., 2003; Mutshinda et al., 2008). Mutshinda et al. (2008) already showed that sizes of local communities fluctuate more than what is expected from neutral theory. This resonates with our simulations of individual species time series which show rather high values of γ (i.e. lower importance of high-frequency fluctuations) when compared to empirical data. Recent progress in population ecology suggests that a promising explanation for these high fluctuations of natural populations might be environmental stochasticity (Lande et al., 2006; Mutshinda et al., 2009), which is absent in neutral models, but not impossible to include in future and more general versions of the original theory (Allen and Savage, 2007).

Realistic slopes of TPL can be produced by a number of different mechanisms (Tokeshi, 1995; Keeling, 2000; Kendal, 2004; Ballantyne and Kerkhoff, 2007) and it is therefore difficult to infer any definitive underlying mechanisms from its shape (Mitzenmacher, 2003). Here we add neutral models to the list of possible mechanisms that can produce realistic TPL slopes, although not necessarily realistic fits.

In conclusion, our results show that realistic slopes of Taylor's power law and density dependence can emerge from a simple neutral model, whilst spectral colors are less likely, but still possible to be reproduced by the neutral model. Still some other natural phenomena remain unexplained by our model, such as the possibility for very small γ closer to white noise. Our findings suggest the interesting possibility that the properties of population time series observed in nature are in part due to simple factors such as sampling effects and dispersal limitation, which would then represent the most parsimonious explanation of observed patterns. The patterns of population fluctuations observed in nature may not reflect resource-driven species-specific dynamics but instead processes at the metacommunity scale, with an important effect of stochastic mortality and random immigration of individuals into local communities. The neutral model encompasses these factors without being overly complex and we therefore suggest that neutral models make more powerful null models for time series data compared to alternatives such as Brownian random walks.

Acknowledgments

References

Allen, A.P., Savage, V.M., 2007. Setting the absolute tempo of biodiversity dynamics. Ecol. Lett. 10, 637–646.

Alonso, D., Etienne, R.S., McKane, A.J., 2006. The merits of neutral theory. Trends Ecol. Evol. 21, 451–457, doi:10.1016/j.tree.2006.03.019.

Anderson, R.M., Gordon, D.M., Crawley, M.J., Hassell, M.P., 1982. Variability in the abundance of animal and plant species. Nature 296, 245–296.

Arino, A., Pimm, S.L., 1995. On the nature of population extremes. Evol. Ecol. 9, 429–443.

Azaele, S., Pigolotti, S., Banavar, J.R., Maritan, A., 2006. Dynamical evolution of ecosystems. Nature 444, 926–928.

Ballantyne, F., Kerkhoff, A.J., 2007. The observed range for temporal mean-variance scaling exponents can be explained by reproductive correlation. Oikos 116, 174–180.

Brook, B.W., Bradshaw, C.J.A., 2006. Strength of evidence for density dependence in abundance time series of 1198 species. Ecology 87, 1445–1451.

Bulmer, M.G., 1974. A statistical analysis of the 10-year cycle in Canada. J. Anim. Ecol. 43, 701–718.

Chave, J., 2004. Neutral theory and community ecology. Ecol. Lett. 7, 241–253.

Dennis, B., Taper, M.L., 1994. Density dependence in time series observations of natural populations: estimation and testing. Ecol. Monogr. 64, 205–224.

Dornelas, M., Connolly, S.R., Hughes, T.P., 2006. Coral reef diversity refutes the neutral theory of biodiversity. Nature 440, 80–82.

Eberhardt, L.L., 1970. Correlation, regression and density dependence. Ecology 51, 306–310.

Etienne, R.S., 2005. A new sampling formula for neutral biodiversity. Ecol. Lett. 8, 253–260.

Etienne, R.S., Haegeman, B. The neutral theory of biodiversity with random fission speciation. Theoret. Ecol. (in press).

Freckleton, R.P., Watkinson, A.R., Green, R.E., Sutherland, W.J., 2006. Census error and the detection of density dependence. J. Anim. Ecol. 75, 837–851.

Gotelli, N.J., McGill, B.J., 2006. Null versus neutral models: what's the difference? Ecography 29 793–800.

Haegeman, B., Etienne, R.S., 2010. Self-consistent approach for neutral community models with speciation. Phys. Rev. E 81, 031911.

Halley, J.M., 1996. Ecology, evolution and 1/f-noise. Trends Ecol. Evol. 11, 33–37, doi:10.1016/0169-5347(96)81067-6.

Hanski, I., Foley, P., Hassell, M., 1996. Random walks in a metapopulation: how much density dependence is necessary for long-term persistence? J. Anim. Ecol. 65 274–282.

Herben, T., Mandák, B., Bímová, K., Münzbergová, Z., 2004. Invasibility and species richness of a community: a neutral model and a survey of published data. Ecology 85, 3223–3233.

Herben, T., 2009. Invasibility of neutral communities. Basic Appl. Ecol. 10, 197–207, doi:10.1016/j.baae.2008.08.006.

Hubbell, S.P., 2001. The Unified Neutral Theory of Biodiversity and Biogeography. Princeton University Press, Princeton.

Hubbell, S.P., Lake, J.K., 2003. The neutral theory of biodiversity an biogeography, and beyond. In: Blackburn, T.M., Gaston, K.J. (Eds.), Macroecology: Concepts and Consequences. Blackwell, Oxford, pp. 45–63.

Inchausti, P., Halley, J., 2001. Investigating long-term ecological variability using the global population dynamics database. Science 293, 655–657.

Inchausti, P., Halley, J., 2002. The long-term temporal variability and spectral colour of animal populations. Evol. Ecol. Res. 4, 1033–1048.

Keeling, M.J., 2000. Simple stochastic models and their power-law type behaviour. Theor. Popul. Biol. 58, 21–31, doi:10.1006/tpbi.2000.1475.

Kendal, W.S., 2004. Taylor's ecological power law as a consequence of scale invariant exponential dispersion models. Ecol. Complex. 1, 193–209, doi:10.1016/j.ecocom.2004.05.001.

Lande, R., Engen, S., Saether, B.-E., 2006. Stochastic Population Dynamics in Ecology and Conservation. Oxford University Press, Oxford.

Legendre, P., Legendre, L., 2003. Numerical Ecology. Elsevier, Amsterdam.

Leibold, M.A., McPeek, M.A., 2006. Coexistence of the niche and neutral perspectives in community ecology. Ecology 87, 1399–1410.

Leigh, E.G., 2007. Neutral theory: a historical perspective. J. Evolution. Biol. 20, 2075–2091.

McGill, B.J., 2003. A test of the unified neutral theory of biodiversity. Nature 422, 881–885.

McGill, B.J., Maurer, B.A., Weiser, M.D., 2006. Empirical evaluation of neutral theory. Ecology 87, 1411–1423.

Miramontes, O., Rohani, P., 2002. Estimating $1/f^\alpha$ scaling exponents from short time-series. Physica D 166, 147–154, doi:10.1016/S0167-2789(02)00429-3.

Mitzenmacher, M., 2003. A brief history of generative models for power laws and lognormal distributions. Internet Mathematics 1, 226–251.

Murdoch, W.W., 1994. Population regulation in theory and practice. Ecology 75, 271–287.

Mutshinda, C.M., O'Hara, R.B.O., Woiwod, P., 2008. Species abundance dynamics under neutral assumptions: a Bayesian approach to the controversy. Funct. Ecol. 22, 340–347.

Mutshinda, C.M., O'Hara, R.B.O., Woiwod, P., 2009. What drives community dynamics? Proc. Roy. Soc. B Biol. Sci. 276, 2923–2929.

Pollard, E., Lakhani, K.H., Rothery, P., 1987. The detection of density-dependence from a series of annual censuses. Ecology 68, 2046–2055.

Rosindell, J., Cornell, S.J., 2007. Species-area relationships from a spatially explicit neutral model in an infinite landscape. Ecol. Lett. 10, 586–595.

Rosindell, J., Cornell, S.J., 2009. Species-area curves, neutral models, and long-distance dispersal. Ecology 90, 1743–1750.

Rosindell, J., Cornell, S.J., Hubbbell, S.P., Etienne, R.S., 2010. Protracted speciation revitalizes the neutral theory of biodiversity. Ecol. Lett. 13, 716–727, doi:10.1111/j.1461-0248.2010.01463.x.

Rosindell, J., Wong, Y., Etienne, R.S., 2008. Coalescence models for spatial neutral ecology. Ecol. Inform. 90, 1743–1750, doi:10.1016/j.ecoinf.2008.05.001.

Shenk, T.M., White, G.C., Burnham, K.P., 1998. Sampling-variance effects on detecting density dependence from temporal trends in natural populations. Ecol. Monogr. 68, 445–463.

Sibly, R.M., Barker, D., Hone, J., Pagel, M., 2007. On the stability of populations of mammals, birds, fish and insects. Ecol. Lett. 10, 970–976.

Taylor, L.R., 1961. Aggregation, variance and the mean. Nature 189, 732–735.

Taylor, L.R., Woiwod, I.P., 1980. Temporal stability as a density-dependent species characteristic. J. Anim. Ecol. 49, 209–224.

Taylor, L.R., Woiwod, I.P., 1982. Comparative synoptic dynamics. I. Relationships between inter- and intra-specific spatial and temporal variance/mean population parameters. J. Anim. Ecol. 51, 879–906.

Taylor, L.R., Taylor, R.A.J., Woiwod, I.P., Perry, J.N., 1983. Behavioural dynamics. Nature 303, 801–804.

Tilman, D., 2004. Niche tradeoffs, neutrality, and community structure: a stochastic theory of resource competition, invasion, and community assembly. Proc. Natl. Acad. Sci. USA 101, 10854–10861.

Tokeshi, M., 1995. On the mathematical basis of the variance-mean power relationship. Res. Popul. Ecol. 37, 43–48.

Turnbull, L.A., Manley, L., Rees, M., 2005. Niches, rather than neutrality, structure a grassland pioneer guild. Proc. Roy. Soc. B, Biol. Sci. 272, 1357–1364.

Volkov, I., Banavar, J.R., Hubbell, S.P., Martian, A., 2003. Neutral theory and relative species abundance in ecology. Nature 424, 1035–1037.

Volkov, I., Banavar, J.R., He, F., Hubbell, S.P., Maritan, A., 2005. Density dependence explains tree species abundance and diversity in tropical forests. Nature 438, 658–661.

Volkov, I., Banavar, J.R., Hubbell, S.P., Maritan, A., 2007. Patterns of relative species abundance in rainforests and coral reefs. Nature 450, 45–49.

Woiwod, I.P., Hanski, I., 1992. Patterns of density dependence in moths and aphids. J. Anim. Ecol. 61, 619–629.